Variation of Size at Maturity of Female Hawksbill Turtles (*Eretmochelys imbricata*), with Speculations on Life-History Tactics Relative to Proper Stock Management

W. N. WITZELL

Reprinted from Japanese Journal of Herpetology 11 (2)

December, 1985

on Biological Aspects of Optimal Strategy and Social Structure from the Japan Ministry of Education, Science and Culture.

REFERENCES

Goris, R.C. 1971. Geographic variation in color and pattern of *Rhabdophis tigrinus* (Boie). Snake 3(1) : 57–59.

Imaizumi, Y. 1957. A classification of *Natrix tigrina* based on variation in the number of scutes. Shizen Kagaku to Hakubutsukan 24(9–10) : 11–19. (in Japanese)

Maki, M. 1931a. A monograph of the snakes of Japan. Dai-ichi Shobo, Tokyo. 247p.

Maki, M. 1931b. Illustrated monograph of the snakes of Japan in color. Dai-ichi Shobo, Tokyo. 248p. (in Japanese)

Maki, M. 1931c. Illustrated monograph of the snakes of Japan. A taxonomical study. Dai-ichi Shobo, Tokyo. 57p. (in Japanese)

Mori, A. and H. Ota. 1984. Growth in the hatchlings of *Rhabdophis t. tigrinus* in captivity. Jpn. J. Herpetol. 10(4) : 118. (in Japanese)

Nakamura K. and S.-I. Uéno. 1963. Japanese reptiles and amphibians in colour. Hoikusha, Osaka. 214p. (in Japanese)

Stejneger, L. 1907. Herpetology of Japan and adjacent territory. Bull. U.S. Natl. Mus. 58 : 1–577.

Wang, C.S. and Y.M. Wang. 1956. The reptile (*sic*) of Taiwan. Q. J. Taiwan Mus. 9 : 1–86.

要　　約

タイワンヤマカガシの第4番目の標本　　太田　英利・森　哲

1984年10月10日，台湾の花蓮県大禹嶺（標高 2,500m）でタイワンヤマカガシ *Rhabdophis tigrinus formosanus* の第4番目の標本を採集し，本亜種が台湾北部にも分布することを再確認した。

本亜種は基亜種に比べて尾下板数の多いことが標徴とされてきたが，この形質は基亜種のそれと重複する部分があり，鑑別点としては，背面の黒斑列が5列あること（基亜種では3～4列）がより有効と考えられる。

Japanese Journal of Herpetology 11(2) : 46-51. 1985.

Variation of Size at Maturity of Female Hawksbill Turtles (*Eretmochelys imbricata*), with Speculations on Life-History Tactics Relative to Proper Stock Management

W. N. WITZELL

ABSTRACT: The mean nesting sizes, and subsequent reproductive rates, of Arabian Peninsula hawksbill turtles (*Eretmochelys imbricata*) are significantly smaller than other hawksbill populations. These differences can not presently be explained due to the lack of basic life history information and, consequently, resource managers are unable to realistically manage any hawksbill population. Research, although costly and time consuming, must be initiated to obtain the demographic data needed; age at maturity, sex ratios, mortality, recruitment, migratory patterns, nesting intervals, philopatry, and whether hatchlings return as adults to reproduce on their natal beaches.

INTRODUCTION

The reproductive strategies of sea turtles are poorly understood because their oceanic habitat makes turtles difficult to study. Many life history parameters, such as age at maturity, sex ratios, mortality, recruitment, migratory patterns, nesting intervals, philopatry, and whether hatchlings return as adults to reproduce on their natal beaches, are unknown. To understand the complex ecology and adaptive significance of various sea turtle life history parameters, biologists must provide comprehensive reproductive data from all nesting populations. Additionally, they must also develop methodologies to collect unknown life history parameters and ecological relationships of these turtles over their entire life span. Only when these parameters are known can these endangered turtle populations be properly managed. Unfortunately, qualitative biologists still sit on beaches counting eggs and quantitative biologists doggedly sit at computer terminals analyzing these data. Research, although costly, must be innovative and tenaciously pursued to obtain the demographic data needed for realistic sea turtle management.

The hawksbill turtle (*Eretmochelys imbricata*) is an interesting example of poorly directed research. The hawksbill, valued commercially for its meat and tortoise shell, is perhaps the least understood of all sea turtles. Variation in mean sizes at

National Marine Fisheries Service, Southeast Fisheries Center, 75 Virginia Beach Drive, Miami, FL 33149, U.S.A.

maturity occurs in different nesting populations, with subsequent differences in reproductive rates, suggesting that there is selection of optimal reproductive sizes in response to varying biological, behavioral, or environmental factors.

Table 1. Straight-line carapace lengths and clutch sizes of seven hawksbill nesting populations.*

Location	Carapace Length (cm)	Number of Eggs per Nest	Source
ATLANTIC OCEAN			
Costa Rica			Carr et al. (1966)
Mean	83.1	161.1	
Range	74.9–91.4	53–206	
Sample	62	57	
Guyana			Pritchard (1969)
Mean	83.8	158.1	
Range	80.0–88.9	138–176	
Sample	23	7	
PACIFIC OCEAN			
Solomon Islands			McKeown (1977)
Mean	80.5	137.5	
Range	68.0–93.0	75–250	
Sample	85	175	
Australia			Limpus (1980)
Mean	76.4	111.7	
Range	71.6–82.7	62–142	
Sample	10	29	
INDIAN OCEAN			
Oman			Ross (1981)
Mean	73.3	97.2	
Range	60.0–83.0	75–118	
Sample	48	9	
South Yemen			Hirth & Carr (1970)
Mean	69.4	81.2	
Range	63.5–72.4	66–99	
Sample	15	5	
PACIFIC OCEAN			
Sudan			Hirth & Latif (1980)
Mean	66.0	73.2	
Range	53.3–73.7	32–117	
Sample	42	26	

* Data are from populations with 10 or more turtles with straight-line carapace measurements.

MATRUE SIZE AND REPRODUCTIVE RATE

The mean sizes of nesting hawksbill turtles are often different between populations (Table 1). These differences reflect different sizes at maturity providing hawksbills essentially stop growing when maturity is reached as occurs in the green turtle (*Chelonia mydas*) (Carr and Goodman, 1970; Bjorndal, 1980; Wood and Wood, 1980). The hawksbill nests in many locations around the world, but reproductive data are scarce (Witzell, 1983). The data presented here represent the seven most complete studies. Mean sizes of nesting hawksbill populations (Table 1) vary from 66.0cm (Sudan) to 83.1cm (Costa Rica). The importance of mean nesting size is apparent when assessing the reproductive rate, because the reproductive rate is positively correlated to the mean size of nesting females (Fig. 1). The number of eggs per clutch produced by hawksbills in Costa Rica, Guyana, Australia, and the Solomon Islands are considerably greater than the number produced by the turtle populations in the Arabian Peninsula, and since eggs sizes are similar (3.8–4.0cm) the differences in the number of eggs laid per clutch between hawksbill populations are actual differences in reproductive output. Also, there is no indication that the populations

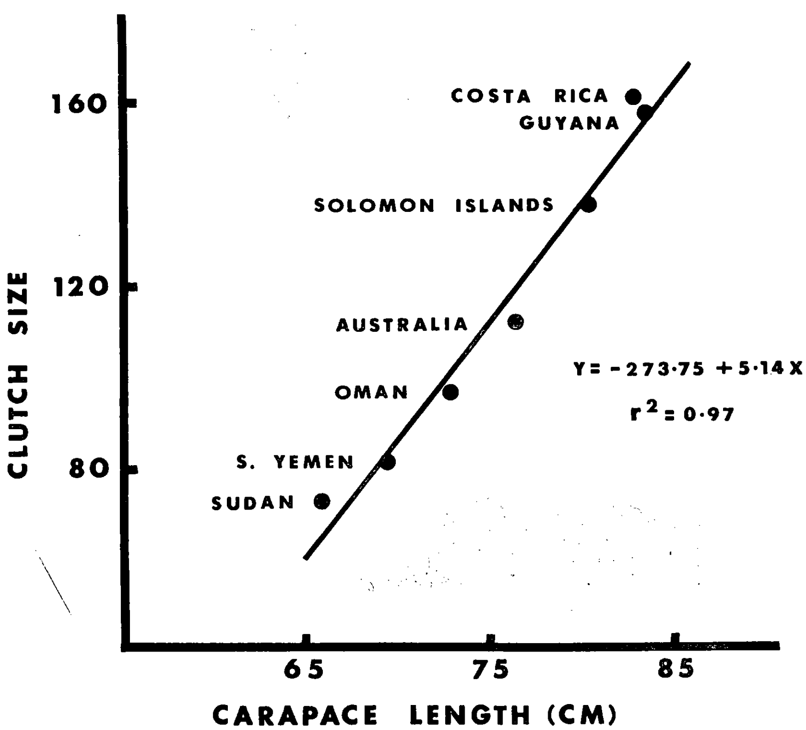

Fig. 1. Linear regression analyses of mean straight-line carapace length and mean clutch size of seven nesting hawksbill sea turtle populations.

of smaller turtles lay as many eggs per season as those populations of larger turtles because the estimated number of nests per turtle per season is two for most populations studied, including Costa Rica, Solomon Islands, and Oman. Unfortunately, there are no comparative multi-year nesting data available for these nesting populations.

The differences in reproductive rates between nesting Arabian and non-Arabian hawksbills illustrate the divergence that can occur in a widely distributed species that consists of independently breeding populations. Presuming that all stable animal populations produce the number of eggs that result in the optimal number of young surviving to reproduce and continue the populations (Lack, 1954, 1966), then why are the reproductive strategies of those hawksbill populations surrounding the Arabian Peninsula different from the other hawksbill populations?

The most important factor offsetting the disadvantage of smaller mature size (and fewer eggs per turtle) is early maturity, which maximizes the number of hatchlings at an early age. This increases evolutionary fitness in several species (Cole, 1954; Meats, 1971; Stearns, 1976). Assuming that wild hawksbill growth rates are similar, and they essentially stop growing at maturity, then do the small-sized Arabian Peninsula populations reach maturity at an earlier age than the other hawksbill populations?

Are there advantages to being small and laying smaller clutches? Do smaller hawksbills indeed nest faster, thereby avoiding the desiccation and intense predation pressure (harassment?) that larger turtles must endure? Perhaps smaller clutches incubate faster or have higher hatching rates than larger clutches, as occurs in other sea turtle species (Ackerman, 1980; Balasingam, 1967).

REPRODUCTIVE SELECTION PRESSURES

The frequently hypersaline environment of the Red Sea area probably had an effect on the evolution of Sudan and Yemen hawksbill populations. The Red Sea is unique in that it has a relatively high degree of faunal depauperacy and endemism. This is a result of paleogeographical processes during the Pleistocene when complete isolations of the Red Sea were caused by fluctuations of the sea level, resulting in a high rate of evolutionary changes (Klausewitz, 1972; Johnson and Feltes, 1984).

It has been speculated that short-term upwellings of cold water inhibit turtle growth or regulate the food supply (Ross, 1980), even though the Sudanese turtles do not undergo this phenomenon. Perhaps the Arabian hawksbills are small because they do not migrate long distances, and therefore do not need large bodies necessary to store sufficient energy needed for both migration and egg production, as occurs in other sea turtles (Carr and Goodman, 1970). Interestingly, some of the clutches in Costa Rica and the Solomon Islands contain variable numbers of small, shelled yolkless lumps but all of the Arabian clutches have large numbers of these lumps. Perhaps these large numbers of lumps laid in each Arabian clutch are, in fact, a vestige of a genetic propensity for traveling long distances and laying larger clutches. Perhaps an extremely high predation rate of subadults and adults in the Arabian area by the numerous sharks (Cousteau and Cousteau, 1970; Steinitz, 1973; Pillai and Honma, 1978) has helped select for early maturity at a smaller size.

CONCLUSION

Divergent reproductive strategies of independently breeding hawksbill populations are not surprising, considering the flexibility of this species (Witzell 1983). The hawksbill is possibly the most adaptive of all sea turtles, these flexible traits enabling individual populations to evolve diverse life history tactics. These diverse life history tactics ensure species dissemination and survival.

However, it is fairly obvious that sea turtle researchers have not only failed at understanding these tactics and underlying mechanisms, but have failed at even addressing basic life history information. Without parameters such as knowing age at maturity, migratory patterns, nesting intervals, philopatry, and whether hatchlings return as adults to reproduce on their natal beaches, resource managers will never be able to properly manage these important species.

LITERATURE CITED

Ackerman, R. 1980. Physiological and ecological aspects of gas exchange by sea turtle eggs. Am. Zool. 20(3) : 575-583.

Balasingam, E. 1967. The ecology and conservation of the Leathery turtle, *Dermochelys coriacea* (Linn.) in Malaya. Proc. 11th. Pacific Science Congress, Tokyo, p. 37-43.

Bjorndal, K. 1980. Demography of the breeding population of the green turtle, *Chelonia mydas*, at Tortuguero, Costa Rica. Copeia 1980 (3) : 525-530.

Carr, A. and D. Goodman. 1970. Ecologic implications of size and growth in *Chelonia*. Copeia 1970 (4) : 783-786.

Carr, A., H. Hirth and L. Ogren. 1966. The ecology and migrations of sea turtles. 6. The hawksbill turtle in the Caribbean Sea. Am. Mus. Novit. 2248 : 1-29.

Cole, L. 1954. The population consequences of life history phenomena. Q. Rev. Biol. 29(2) : 103-137.

Cousteau, J.Y. and P. Cousteau. 1970. The shark: splendid savage of the sea. Doubleday and Co., Inc., New York.

Hirth, H. and A. Carr. 1970. The green turtle in the Gulf of Aden and the Seychelles Islands. Verh. K. Ned. Akad. Wet. 58(5) : 1-44.

Hirth, H. and E. Latif. 1980. A nesting colony of the hawksbill turtle *Eretmochelys imbricate* on Seil Ada Kebir Island, Suakin Archipelago, Sudan. Biol. Conserv. 17(2) : 125-130.

Johnson, R. and R. Feltes. 1984. A new species of *Vinciguerria* (Salmoniformes: Photichthyidae) from the Red Sea and the Gulf of Aqaba, with comments on the depauperacy of the Red Sea mesopelagic fish fauna. Fieldiana Zool. (N.S.) 22 : 35p.

Klausewitz, W. 1972. The zoogeographical and paleogeographical problem of the Indian Ocean and the Red Sea according to ichthyofauna of the littoral. J. Mar. Biol. Assoc. India. 14(2) : 697-706.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, London.

Lack, D. 1966. Population studies of birds. Clarendon Press, London.

Limpus, C. 1980. Observations on the hawksbill turtle (*Eretmochelys imbricata*) nesting along the Great Barrier Reef. Herpetologica 36(3) : 265-271.

McKeown, A. 1977. Marine turtles of the Solomon Islands. Ministry of Natural Resources, Fisheries Division, Honiara, 47p.

Meats, A. 1971. The relative importance to population increase of fluctuations in mortality, fecundity, and the time variables of the reproductive schedule. Oecologia 6 : 223-237.

Pillai, P. and M. Honma. 1978. Seasonal and areal distribution of the pelagic sharks taken by the tuna longline in the Indian Ocean. Bull. Far Seas Fish Res. Lab. 16 : 33-48.

Pritchard, P. 1969. Sea turtles of the Guianas. Bull. Fla. State Mus. Biol. Sci. 13(2)85-140.

Ross, J. 1981. Hawksbill turtle *Eretmochelys imbricata* in the Sultanate of Oman. Biol. Conserv. 19(2) : 99-106.

Stearns, S. 1976. Life-history tactics: A review of the ideas. Q. Rev. Biol. 51(1) : 3-47.

Steinitz, H. 1973. Fish ecology of the Red Sea and Persian Gulf. *In* B. Zeitschel (ed.), The biology of the Indian Ocean. Ecol. Ser. 3, p. 465-466. Springer-Verlag, New York.

Witzell, W. 1983. Synopsis of biological data on the hawksbill turtle *Eretmochelys imbricata* (Linnaeus, 1766). FAO Fish. Synop. 137 : 78p.

Wood, J. and F. Wood. 1980. Reproductive biology of captive green sea turtles *Chelonia mydas*. Am. Zool. 20(3) : 499-505.

要　　旨

雌タイマイの成熟時の大きさの変異　　W. N. ウィッツェル

アラビア半島のタイマイの産卵個体の平均は他地域の個体群と比べて有意に小さく，繁殖率も同様に低い。この理由は生活史の基礎資料が不足のため，いまのところ説明できない。経費がかかり時間もかかるが，これら生活史の資料を得るための研究が必要である。